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Phylogeny and metabolic scaling in mammals

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Abstract. The scaling of metabolic rates to body size is widely considered to be of great biological and ecological importance, and much attention has been devoted to determining its theoretical and empirical value. Most debate centers on whether the underlying power law describing metabolic rates is 2/3 (as predicted by scaling of surface area/volume relationships) or 3/4 ("Kleiber's law"). Although recent evidence suggests that empirically derived exponents vary among clades with radically different metabolic strategies, such as ectotherms and endotherms, models, such as the metabolic theory of ecology, depend on the assumption that there is at least a predominant, if not universal, metabolic scaling exponent. Most analyses claimed to support the predictions of general models, however, failed to control for phylogeny. We used phylogenetic generalized least-squares models to estimate allometric slopes for both basal metabolic rate (BMR) and field metabolic rate (FMR) in mammals. Metabolic rate scaling conformed to no single theoretical prediction, but varied significantly among phylogenetic lineages. In some lineages we found a 3/4 exponent, in others a 2/3 exponent, and in yet others exponents differed significantly from both theoretical values. Analysis of the phylogenetic signal in the data indicated that the assumptions of neither species-level analysis nor independent contrasts were met. Analyses that assumed no phylogenetic signal in the data (species-level analysis) or a strong phylogenetic signal (independent contrasts), therefore, returned estimates of allometric slopes that were erroneous in 30% and 50% of cases, respectively. Hence, quantitative estimation of the phylogenetic signal is essential for determining scaling exponents. The lack of evidence for a predominant scaling exponent in these analyses suggests that general models of metabolic scaling, and macro-ecological theories that depend on them, have little explanatory power.

Key words: allometry; basal metabolic rate (BMR); field metabolic rate (FMR); Kleiber's law; metabolic theory of ecology (MTE); phylogenetic comparative analysis; phylogenetic generalized least squares; phylogenetically independent contrasts; phylogeny; power law; scaling.

Introduction

The empirical values of scaling exponents relating physiological variables to body size are held to reflect important general constraints (Schmidt-Nielsen 1984, Peters 1986, O'Connor et al. 2007; see also Dodds et al. [2001] and Glazier [2005] for reviews on the scaling of metabolic rates). The scaling of energy needs has generated particular interest, as it potentially has major implications for organisms' population densities, ecology and behavior (Peters 1986, Lovegrove 2000, Dodds et al. 2001, Anderson and Jetz 2005, McNab 2005*a*, *b*, 2006, Duncan et al. 2007, White et al. 2007*b*, Dial et al. 2008). An early theoretical model proposes that metabolic rate of organisms maintaining a constant body temperature is proportional to the rate of heat loss through their body surface area. Because surface area scales to the two-thirds power of volume and mass, the model predicts that the allometric exponent of metabolic rate on body mass is two-thirds, or 0.66 (reviewed in Schmidt-Nielsen [1984] and Dodds et al. [2001]; see also Reynolds 1997). A seminal paper by Kleiber, however, concluded that mammalian basal metabolic rate (BMR) scales on body mass with a 0.75 exponent ("Kleiber's law," reviewed by Schmidt-Nielsen [1984] and Dodds et al. [2001]). Ever since, theoretical models have been proposed to explain the 3/4 scaling of metabolism, such as dimensional analysis-based models (reviewed by Schmidt-Nielsen [1984] and Dodds et al. [2001]), nutrient supply network (West et al. 1997), four-dimensional biology (West et al. 1999), and allometric cascade models linking physiological processes from cell level to whole organism level (Darveau et al. 2002). Because early empirical studies suggested that the three-quarter scaling of metabolism is found from unicellular organisms to mammals, several models rest on the assumption of an underlying 3/4 scaling principle (West et al. 1997, 1999, Gillooly et al. 2001). Recently, it has been proposed that the 3/4 scaling of metabolism can also explain a range of interspecific macroecological and life history patterns (the "metabolic theory of ecology," MTE; Brown et al. 2004).

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While these models sparked discussion about the 3/4 allometric exponent of metabolism (Dodds et al. 2001, Banavar et al. 2002, 2003, Darveau et al. 2002, 2003, West et al. 2002*a*, *b*, 2003), recent empirical studies have further tested the assumptions on which the models rest, especially that the allometric exponent (*b*) is indeed 0.75. Savage and colleagues (2004) found $b = 0.75$ in most taxonomic groups (plants, birds, fish), Farrell-Gray and Gotelli (2005) supported a 3/4 exponent only for endotherms but not for ectotherms, while other authors concluded that the 3/4 exponent may differ between broad taxonomic groups (from unicellular organisms to plants to all vertebrate classes; White et al. 2007*a*, Glazier 2008). Similarly, the allometric slope of field metabolic rate (FMR) is believed to be 0.75 (Nagy et al. 1999, Anderson and Jetz 2005), but there has been little/no attention to the variability or otherwise of this value. This is surprising because, while BMR is recorded under conditions that animals rarely meet in the wild, FMR is an estimate of the daily energy expenditure under natural conditions, and therefore a more meaningful estimate of metabolism.

Differences in conclusions between studies might be determined by the choice of methods and species included in the analyses. Here we mention a few examples among the most influential recent papers in the field to illustrate the diversity of approaches used and conclusions reached. Because most BMR data come from small mammals, data sets are sometimes analyzed separately for "small" and "large" mammals, but the threshold used to split the data set is arbitrary. By dividing the data sets in multiple subsets Dodds et al. (2001) concluded that the allometric exponent of BMR varies across the range of body sizes and that there is a threshold at 10 kg, such that a 2/3 scaling exponent is found in mammals of mass less than 10 kg (and in birds), while larger mammals have a 3/4 exponent, thus leading to a general "mammalian" slope between the two predicted values. Savage et al. (2004) instead partitioned the data in size-classes ("bins"), averaged values of all species within each class and used these means in their analysis of scaling exponents. This approach however reduces sample sizes and thus statistical power and, like the previous example, also ignores the influence of phylogeny. Finally, White and Seymour (2003, 2005) normalized BMR to the mean body temperature across species prior to the analysis, arguing that "body mass and body temperature are the primary determinants of metabolic rate" (White and Seymour 2003:4046, White and Seymour 2005:1615). Hence, it is currently unclear whether variability in scaling exponents reflects methodology or biological reality.

A crucial consideration in comparative analyses is the need to control for nonindependence in the data due to phylogeny (Felsenstein 1985, Harvey and Pagel 1991, Nunn and Barton 2001, Garland et al. 2005). Although simulations have shown that ignoring the "phylogenetic signal" (Blomberg and Garland 2002) in the data leads to erroneous conclusions (Martins and Garland 1991), a large number of empirical studies on the allometry of metabolic rates ignored phylogeny and were conducted at the species level (Heusner 1991, Dodds et al. 2001, Gillooly et al. 2001, Savage et al. 2004) or only partially controlled for similarity between species due to their common ancestry (White and Seymour 2003, McNab 2008). White and Seymour (2003), for example, assessed the association between traits across orders, which, like species, are not statistically and phylogenetically independent units (Harvey and Pagel 1991); their approach also reduced greatly sample sizes ($n = 17$). One recent phylogenetic comparative study of BMR concluded that "the 95% confidence intervals included, or almost included, the scaling exponent predicted by MTE" (Duncan et al. 2007), though the predictions of the MTE for the scaling of age at first reproduction and growth rate did not hold (Duncan et al. 2007, Lovegrove 2009).

Here we investigated the importance of using phylogenetic comparative methods when studying the scaling of both basal metabolic rate and the ecologically more relevant measure, field metabolic rate in mammals, and assessed how the choice of method affects the conclusions regarding the proposed theoretical exponents. We also tested for differences between clades to assess the variability of the exponent within mammals. For each clade and metabolic rate, we first tested whether there is a phylogenetic signal in metabolic rates and in their association with body mass (Blomberg and Garland 2002, Freckleton et al. 2002, Blomberg et al. 2003), and derived the slopes under different models that accounted for phylogeny to a different extent. Second, we tested whether models that did not account for phylogeny (species-level analysis) fit the data better than models that accounted for phylogeny.

Methods

Data collection

We used the BMR database of White and Seymour (2003) and White et al. (2006) for mammals. Data were used as estimates of BMR (in mL O_2/hour) if measurements were collected on adult, nonreproducing, postabsorptive, resting and inactive but not sleeping individuals, and with external temperature within the thermoneutral zone for the species (McNab 1988, 1997). Data that did not fulfill these criteria were discarded. However, we excluded from this data set nine primates whose BMR estimates were not measured under the conditions explained above (Ross 1992). Overall, the BMR data set included 580 mammals.

We enlarged the mammalian data set in Nagy et al. (1999) on FMR with new data published since 1999. Data on FMR (kJ/d) were included in the analysis if collected with the doubly labeled water method on wild adult individuals. The final FMR data set included 119 species. All the data were log-transformed prior to

statistical analysis (data set available in Supplement; references in Appendix A).

Phylogenetic signal and estimating allometric exponents

We used Bininda-Emonds et al. (2007) super-tree of mammals with updated branch lengths (Bininda-Emonds et al. 2008) and BayesTraits (Pagel et al. 2004) for all statistical analyses. Because the use of phylogenetically controlled methods has been questioned when applied to the study of metabolism (e.g., Westoby et al. 1995, McNab 2005*a*, *b*, 2006, 2008), we first assessed the strength of the phylogenetic signal (λ) for BMR and FMR alone and then for their association with body mass, using phylogenetic generalized least-squares models (PGLS; Pagel 1997, 1999, Blomberg and Garland 2002, Freckleton et al. 2002, Blomberg et al. 2003, Lavin et al. 2008) in BayesTraits (Pagel et al. 2004). A simulation study showed that λ correctly predicts the strength of phylogenetic signal in the data (Freckleton et al. 2002).

In PGLS, the phylogeny is transformed into a variance–covariance matrix, such that the path length from the root to the tips of the tree (the "variance") is given along the diagonal of the matrix, and the shared evolutionary history of any given pair of species, represented as time of common evolution from the root to the last common ancestor (the "covariance"), is given in the off-diagonal values (Pagel 1999, Freckleton et al. 2002, Lavin et al. 2008). The λ parameter is found by maximum likelihood (ML) in PGLS and potentially varies between 0 (no phylogenetic signal; the species can be treated as independent) and 1 (the observed pattern of trait variation among the species is predicted by the phylogeny, i.e., the similarity among species scales in direct proportion to their shared evolutionary time; Pagel 1997, 1999, Freckleton et al. 2002). Mathematically λ scales the off-diagonal values of the variance–covariance matrix (Pagel 1999, Freckleton et al. 2002). When $\lambda = 0$, the off-diagonal values are equal to 0 and the tree becomes a "star" phylogeny (Pagel 1999, Lavin et al. 2008). When $\lambda = 1$, branch lengths remain unaltered; when this model fits the data better we can conclude that the phylogeny correctly predicts the pattern of variation at the tips under a Brownian motion model of evolution (further mathematical details can be found in Pagel 1999, Garland and Ives 2000, Freckleton et al. 2002, Lavin et al. 2008).

We calculated the allometric regression of both BMR and FMR on body mass, while simultaneously estimating ML λ as explained above (Pagel 1997, 1999, Freckleton et al. 2002). Regression parameters were also found with ML in PGLS (Pagel 1997, 1999, Freckleton et al. 2002). In regression, the variance–covariance matrix with λ is incorporated in the error term of the regression equation, so that the error term is partitioned into a component representing the phylogeny and the remaining error term (Pagel 1997, 1999, Freckleton et al. 2002). This allowed us to quantify and account for the strength of the phylogenetic signal in the association of metabolic rates and body mass, and hence, the phylogenetic signal in the residuals, that is, of relative metabolic rates (Pagel 1997, 1999, Freckleton et al. 2002, Lavin et al. 2008, Cooper and Purvis 2009). BMR and FMR were controlled for allometry with body mass of the laboratory (BMR) and wild (FMR) animals, as reported in the data sources. We called $PGLS_\lambda$ these PGLS regression models in which ML λ is estimated.

Regression analyses in which λ was forced to be equal 0 are therefore equivalent to species-level analysis, i.e., ordinary least-square (OLS) regression, while regressions with $\lambda = 1$ produce similar results to those obtained with phylogenetically independent contrasts (PIC) (Pagel 1999, Garland and Ives 2000, Lavin et al. 2008). When ML λ is intermediate between 0 and 1, therefore, both OLS and PIC are not ideal methods, because they respectively underestimate and overestimate the influence of phylogeny. Conversely, $PGLS_\lambda$ offers a more flexible approach by simultaneously estimating ML λ when testing the association between variables with regression analysis, thus accounting for the precise strength of the phylogenetic signal that the data exhibit. Thus, unlike OLS and PIC, $PGLS_\lambda$ does not impose a given value for the phylogenetic signal on the data, but it finds the best-fitting model with the appropriate λ value that could range from 0 to 1.

To identify the best-fitting model, we compared alternative models, i.e., models with $\lambda = \text{ML}$ ($PGLS_\lambda$), $\lambda = 0$ (OLS), and $\lambda = 1$ (PIC), using likelihood ratio (LR) test (where $\text{LR} = -2 \times [\text{Lh (better-fitting model)} - \text{Lh (worse-fitting model)}]$ the best-fitting model having the highest log-likelihood score, Lh), which was tested for significance with a χ^2 distribution with 1 degree of freedom (Pagel 1997, 1999, Freckleton et al. 2002, Lavin et al. 2008).

The analysis was replicated within placentals and marsupials, and within orders with sample sizes larger than 30 (rodents for both BMR and FMR; carnivores, bats, and "true insectivores" [order Lypothyphla] for BMR only). We then compared allometric slopes within and between lineages using *t* tests. Finally, we checked whether results and conclusions about the value of allometric exponents differed when λ was fixed as 0 (as assumed in OLS) or 1 (as assumed in PIC).

Some authors (Speakman et al. 1995, McNab 1997, White and Seymour 2005, Clauss et al. 2008) suggest that BMR cannot be adequately measured in Artiodactyla, Soricidae, Lagomorpha, and Macropodidae, because post-absorptive states might be unachievable in herbivores due to the long time needed for microbial fermentation of cellulose during digestion, while post-absorptive shrews tend to be hyperactive; therefore, estimates of metabolic rate of these species are not physiologically comparable to the "basal" metabolism of other species. White and Seymour (2005) concluded that the inclusion of these mammals in the analysis of the alllometry of BMR inflates the slope from 0.66 to

TABLE 1. Phylogenetic generalized least-squares models (PGLS) analysis on the strength of the phylogenetic signal (λ) of individual traits, specifically field metabolic rate (FMR), basal metabolic rate (BMR), and body mass in mammals.

Trait	ML λ	Lh, λ = ML	Lh, λ = 0	λ = ML vs. λ = 0		Lh λ = 1	λ = ML vs. λ = 1	
				LR	*P*		LR	*P*
FMR ($n = 119$)	0.95	−89.0	−160.0	142.0	<0.0001	−95.27	12.51	0.0004
BMR ($n = 579$)	0.98	−240.8	−616.6	751.6	<0.0001	−264.68	47.76	<0.0001
Body mass for FMR ($n = 119$)	0.98	−118.0	−196.4	157.7	<0.0001	−120.79	5.63	0.018
Body mass for BMR ($n = 579$)	0.99	−380.5	−813.9	866.8	<0.0001	−388.7	16.3	<0.0001

Notes: The first two columns report the maximum likelihood (ML) λ value and the log-likelihood score (Lh) of a model with λ = ML. The following three columns report the Lh when λ is forced to be 0, the LR test for the comparison with the model with λ = ML, and its associated *P* value. The last three columns report the Lh of a model in which λ is forced equal to 1, and the LR test and *P* value for the comparison vs. the model with λ = ML (models with a statistically higher Lh score, as assessed with LR test, provide a better fit to the data). The number of species used in the analyses, *n*, is also reported.

0.75, and argued that species composition of comparative data sets and contamination with non-basal estimates are the factors behind differences in conclusions across studies. We therefore repeated the analysis without Artiodactyla, Soricidae, Lagomorpha, and Macropodidae ("restricted data set").

The statistical basis of the allometric analyses of metabolic rates has recently been challenged by the claim that the log-log relationship across species is not linear (Packard and Birchard 2008). We examined plots of residuals on predicted values to check for possible nonlinearity in the data (Quinn and Keough 2002) and also tested whether a $PGLS_\lambda$ quadratic model provided a better fit to the data. Where we found ML λ was statistically indistinguishable from 1, we also employed phylogenetically independent contrasts (Felsenstein 1985, Harvey and Pagel 1991, Garland et al. 1992) to further assess whether the relationship between metabolic rates and body mass is not linear, since it is possible to fit nonlinear models to contrasts. We computed contrasts in CAIC (Purvis and Rambaut 1995), using real branch lengths to match the PGLS analysis. Bivariate linear regressions of contrasts in metabolic rate on body mass were forced through the origin (Felsenstein 1985, Harvey and Pagel 1991, Garland et al. 1992) and residuals of these regressions checked for evidence of nonlinear relationships against predicted values (Quinn and Keough 2002).

RESULTS

Phylogenetic signal

When tested individually, BMR and FMR showed a ML λ value close to 1 in all lineages (Table 1; Appendix B: Tables B1 and B2). Similarly, ML λ of body mass alone was high for both the BMR and the FMR data set (Table 1; Appendix B: Table B1 and B2). These results indicate that both absolute metabolic rates and body mass taken independently exhibit a strong phylogenetic signal.

Next we estimated the allometric slopes of metabolic rates on body size using $PGLS_\lambda$ regression analysis, hence simultaneously estimating the ML λ value for their association. Although ML λ was high for both absolute metabolic rates and body mass when these were tested individually, ML λ of their regression on body mass was generally lower, indicating that relative metabolic rates have lower phylogenetic signal. Most importantly, the phylogenetic signal of relative metabolic rates differed between lineages. Specifically, ML λ varied between 0.23 (bats) and 1.00 (true insectivores) for relative BMR, and ranged between 0.00 (marsupials) and 1.00 (rodents) for relative FMR (Table 2).

Given the above results, we tested whether the scaling exponent of metabolic rates varied in relation to the strength of the phylogenetic signal (ML λ) of the association between metabolic rates and size. The estimate of the slope of metabolic rates was unrelated to ML λ (Pearson correlation: $r = -0.5$, $df = 7$, $P = 0.20$ for BMR; $r = 0.8$, $df = 3$, $P > 0.10$ for FMR), suggesting that the scaling exponent was not steeper or shallower depending on the strength of the phylogenetic signal of relative metabolic rates.

Allometric exponents of metabolic rates when λ = ML

$PGLS_\lambda$ models showed that the BMR allometric exponent varied between clades (Table 2, Fig. 1a). Specifically, the BMR allometric slope for all mammals excluded both predicted values (0.718; 95% CI, 0.697–0.738), it differed from both 2/3 and 3/4 in placentals and rodents, while 0.75 was supported in marsupials, carnivores and bats, and 0.66 in true insectivores (Table 2; Fig. 1a). As a consequence, comparisons among clades revealed that the BMR slope of true insectivores was lower than those of other mammalian lineages (Table 3; Fig. 1a). In addition, marsupial and placental BMR allometric exponents were not statistically different from one another (Table 3).

FMR allometric exponents also differed between lineages (Table 2, Fig. 1b). Overall, the mammalian FMR slope was not statistically different from a 2/3 exponent. However, our analysis revealed that marsupials had a lower FMR allometric slope than placentals ($t_{112} = 3.92$, $P < 0.001$) that excluded both 2/3 and 3/4, while the FMR slope of placentals included 3/4 (Table 2, Fig. 1b) and the 95% CI of FMR slope in rodents included both predicted values (Table 2). Finally, the allometric exponents of BMR and FMR did not differ

TABLE 2. $PGLS_\lambda$ models for the allometry of FMR and BMR in each clade, with ML λ value for the relationship between metabolic rate and body mass, t value with df and R^2, slopes with 95% confidence intervals.

Clade	FMR					BMR				
	ML λ	t	df†	R^2	b (95% CI)	ML λ	t	df†	R^2	b (95% CI)
Mammalia	0.67	31.57	116	0.89	0.697 (0.653–0.741)	0.85	69.99	576	0.89	0.718 (0.697–0.738)
Eutheria	0.41	27.53	78	0.91	0.735 (0.681–0.788)	0.78	60.25	508	0.88	0.717 (0.694–0.740)
Metatheria	0.00	28.86	34	0.96	0.601 (0.558–0.643)	0.40	49.61	62	0.98	0.724 (0.695–0.753)
Rodentia	1.00	11.70	34	0.80	0.766 (0.633–0.899)	0.69	43.96	263	0.88	0.711 (0.679–0.742)
Carnivora						0.85	21.28	47	0.90	0.773 (0.699–0.846)
Chiroptera						0.23	22.10	73	0.87	0.766 (0.697–0.835)
Lypothyphla						1.00	11.51	35	0.79	0.587 (0.484–0.691)
Restricted data set‡										
All mammals						0.80	68.09	528	0.90	0.718 (0.697–0.739)
Eutheria						0.72	58.89	467	0.88	0.719 (0.695–0.731)
Metatheria						0.36	44.95	56	0.97	0.723 (0.691–0.756)

Note: All tests had a P value <0.0001.

† The df associated with t test.

‡ These analyses were conducted with a restricted data set in which Artiodactyla, Lagomorpha, Soricidae, and Macropodidae were excluded on the assumption that BMR in these species cannot be measured because they may never exhibit the physiological conditions required (see *Methods: Phylogenetic signal and estimating allometric exponent*). The analysis was not repeated for Lypothyphla because the sample size without Soricidae was too small ($n = 13$ species).

from one another within each lineage, with the sole exception of marsupials whose BMR slope was steeper than the FMR slope (Table 4).

Our results remained qualitatively unchanged when artiodactyls, shrews, lagomorphs and macropods were excluded (Tables 2 and 3).

Comparison with slopes estimated when λ = 0 (OLS) and when λ = 1 (PIC)

OLS models ($\lambda = 0$) returned discrepant estimates of allometric slopes in 3 out of 11 tests when compared to $PGLS_\lambda$ models, specifically a lower slope for BMR in rodents (0.67) and true insectivores (0.48, excluding 0.66), and FMR slopes for all mammals (0.71, excluding both 2/3 and 3/4; Table 5). Models with $\lambda = 1$, equivalent to PIC, returned discrepant slopes in 5 out of 11 cases when compared to $PGLS_\lambda$ models (BMR for all mammals, placentals and rodents, FMR in all mammals and marsupials; Table 5). Overall models with $\lambda = 1$ tended to give higher slopes than $PGLS_\lambda$, appearing to indicate support for a 0.75 exponent in most clades.

Comparisons between models indicated that $PGLS_\lambda$ models provided a better fit to the data than both OLS models and PIC, with the exception of few cases in which ML λ was not statistically different from 0 (BMR for marsupials, FMR for marsupials, and FMR for placentals with $PGLS_\lambda$ model vs. OLS model; $P = 0.053$; Table 6) or 1 (BMR for true insectivores, FMR for rodents; Table 6). In such cases, therefore, $PGLS_\lambda$ returned similar slopes as OLS and PIC.

Because $PGLS_\lambda$ models better fit the data, conclusions on the theoretical values of the allometric slopes of metabolic rates should be based on such models rather than on non-phylogenetic OLS or PIC models (equivalent to models in which λ is unrealistically assumed to be either 0 or 1, respectively).

Nonlinearity of the relationship between metabolic rates and body mass

Plots of residuals on predicted values in our analysis show a slight tendency to be U shaped (Appendix C: Fig. C1), but this may be an artefact of phylogenetic nonindependence. Although the $PGLS_\lambda$ slope itself is independent of phylogeny, the residuals are not, because they are computed as the deviation of species values from the $PGLS_\lambda$ regression (e.g., phylogenetic signal of the $PGLS_\lambda$ residuals [relative metabolic rates] in all mammals: BMR $\lambda = 0.85$; FMR $\lambda = 0.67$). To test for nonlinearity it is therefore necessary to control for phylogenetic effects by using $PGLS_\lambda$ to determine the relationship between residuals and predicted values. This shows no significant association between residuals and predicted values across all mammals (BMR, $t_{576} = -0.002$, $P = 0.99$; FMR, $t_{116} = -0.003$, $P = 0.99$). In addition, for clades in which ML $\lambda = 1$ (true insectivores [BMR] and rodents [FMR]; see Table 2), we checked for nonlinearity using residual vs. predicted independent contrasts. There was no evidence of a nonlinear relationship in these analyses (Appendix C: Fig. C2). Finally, we tested whether a $PGLS_\lambda$ model with a quadratic term provided a better fit to the data than a $PGLS_\lambda$ linear model. Although the quadratic term was significant (for BMR, body mass $t_{575} = 18.2$, $P < 0.001$; (body mass)^2 $t_{575} = 3.4$, $P = 0.0006$; for FMR, body mass $t_{115} = 3.7$, $P = 0.0002$; (body mass)^2 $t_{115} = 4.6$, $P < 0.0001$), the R^2 increased by only 0.003 for BMR ($PGLS_\lambda$ linear $R^2 = 0.895$; $PGLS_\lambda$ polynomial $R^2 = 0.898$) and 0.022 for FMR ($PGLS_\lambda$ linear $R^2 = 0.895$; $PGLS_\lambda$ polynomial $R^2 = 0.917$).

DISCUSSION

We can draw two major conclusions from our analysis: (1) allometric slopes vary across mammalian lineages and metabolic rates and neither 2/3 nor 3/4

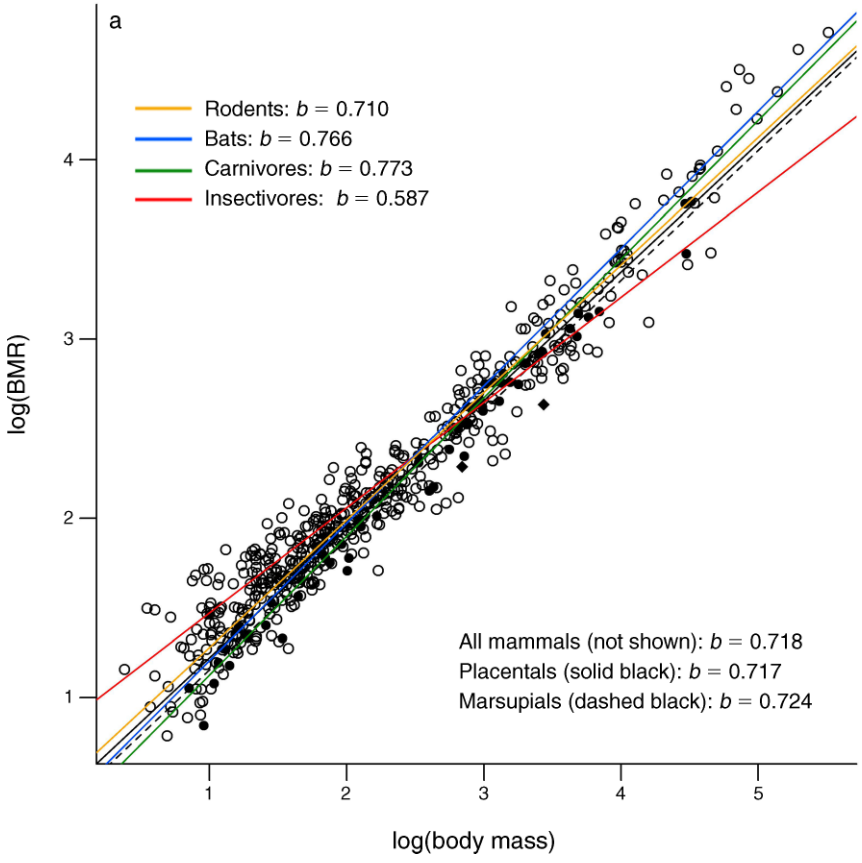

FIG. 1. Relation between metabolic rates and body mass (measured in kg) in mammals: (a) basal metabolic rate (BMR, measured in mL O_2/h) and (b) field metabolic rate (FMR, measured in kJ/d). Key to symbols: open circles, placental mammals; solid circles, marsupials; diamonds, monotremes. Fit lines have been derived from the $PGLS_\lambda$ models and are drawn in solid black for placentals and dashed black for marsupials. In panel (a), fit lines from $PGLS_\lambda$ models are also shown for rodents (yellow), bats (blue), carnivores (green), and insectivores (red). Fit lines for all mammals are not shown. Confidence intervals of the slopes for the $PGLS_\lambda$ fit-lines for each lineage are given in Table 2.

exponents are consistently supported; (2) $PGLS_\lambda$ models, that account for the phylogenetic signal in the data, always fit the data better than OLS models and PIC and should therefore be preferred when studying the allometry and evolution of metabolic rates.

Our $PGLS_\lambda$ analysis shows that allometric slopes for basal and field metabolic rates vary significantly between lineages, and that, in several cases, neither of the commonly proposed values (0.66 and 0.75) can adequately explain the data. The mammalian BMR allometric slope was significantly different from both 0.66 and 0.75. Within clades, the 95% CIs for BMR excluded both values in placentals and rodents, supported 0.75 in carnivores, bats and marsupials, and 0.66 in true insectivores. As a result, true insectivores had shallower BMR slopes than all other lineages. For FMR, a 3/4 exponent was obtained for placentals, but the 95% CIs for marsupials excluded both 2/3 and 3/4. The allometric slopes of BMR and FMR did not differ from one another within each lineage, with the sole exception of marsupials that had a significantly lower FMR slope (0.60) than a BMR slope (0.72). As a result, the FMR slope was significantly lower in marsupials than in placentals, but there was no difference between placentals and marsupials in the BMR slope.

Our results are consistent with and support the conclusions of a previous $PGLS_\lambda$ analysis showing that the mammalian BMR allometric slope excludes both theoretical values ($b = 0.724$; 95% CI, 0.706–0.742 in Duncan et al. 2007) and exhibits variation among lineages (Duncan et al. 2007). Relative to this analysis our estimates for the mammalian BMR slope is slightly lower and far from 3/4 ($b = 0.718$; 95% CI, 0.697–0.734). This is likely to be the consequence of our choice to include only BMR estimates that strictly followed the protocol defined by McNab (1988, 1997), while Duncan et al. (2007) based their analysis on Savage et al. (2004) data set that included estimates of resting metabolic rates (hence values that did not fulfill all the criteria for BMR, and thus might provide higher metabolic rates than basal estimates). In addition we used a recent mammalian phylogeny with branch length in time

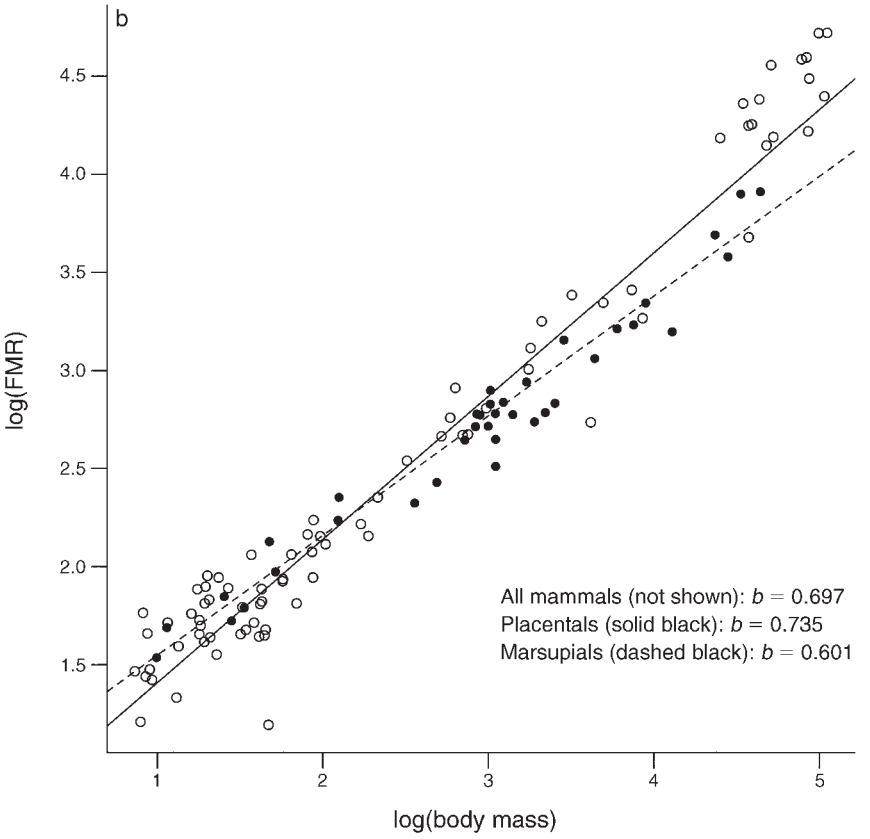

FIG. 1. Continued.

(Bininda-Emonds et al. 2008) instead of a composite tree with arbitrary branch length as in Duncan et al.'s (2007) study.

Our conclusions are robust and do not change once herbivores and shrews are removed from the data set. Thus, contrary to previous claims (White and Seymour 2003, 2004, 2005, Clauss et al. 2008), exclusion of these species does not yield a slope of 0.66. Given that we used the same data set as White and Seymour (2003), the difference in our results is likely to be due to differences in the analysis, namely, whether or not BMR data are normalized to a common body temperature (as in White and Seymour 2003, 2004, 2005), and/or whether or not the analyses account for phylogenetic nonindependence (as in our analyses). We argue that normalization to a common body temperature is unnecessary because BMR measurements are collected under controlled and physiologically equivalent conditions. The protocol for measuring BMR (McNab 1997) specifies that animals are tested in their thermoneutral zone, and thus not expending energy on thermoregulation. Any subsequent normalization procedure will therefore introduce an error in a species' BMR measurements, even more so because it is done irrespective of phylogeny. Furthermore, normalizing BMR to a common body temperature assumes that a low BMR is a consequence of low

TABLE 3. Comparison of BMR slopes between clades (t statistics with degrees of freedom and P values).

Comparison	t	df	P
Eutheria–Metatheria	0.36	570	0.716
Carnivora–Chiroptera	0.14	120	0.889
Rodentia–Carnivora	1.57	310	0.117
Rodentia–Chiroptera	1.43	336	0.154
Lypothyphla–Chiroptera	2.89	108	0.005
Lypothyphla–Carnivora	2.98	82	0.004
Lypothyphla–Rodentia	2.32	298	0.021
Lypothyphla–Metatheria	2.58	97	0.011
Metatheria–Carnivora	1.26	109	0.212
Metatheria–Rodentia	0.59	325	0.554
Metatheria–Chiroptera	1.10	135	0.272

Note: Allometric slopes of $PGLS_\lambda$ models and 95% CI in each lineage are given in Table 2.

TABLE 4. Comparison between FMR and BMR allometric slopes from $PGLS_\lambda$ models within each lineage (t value with degrees of freedom and P value).

Clade	t	df	P
Mammalia	0.87	692	0.385
Eutheria	0.62	586	0.538
Metatheria	4.77	96	<0.0001
Rodentia	0.82	297	0.412

Note: Allometric slopes and 95% CI in each clade are presented in Table 2.

TABLE 5. Estimates of BMR and FMR allometric slopes with 95% confidence intervals (CI, in parentheses) from ordinary least-squares (OLS) regression models ($\lambda = 0$) and phylogenetically independent contrasts (PIC; $\lambda = 1$).

Clade	OLS, $\lambda = 0$	PIC, $\lambda = 1$
BMR		
Mammalia	0.691 (0.677–0.704)	0.743 (0.717–0.769)
Eutheria	0.691 (0.676–0.706)	0.746 (0.717–0.776)
Metatheria	0.735 (0.711–0.759)†	0.728 (0.686–0.770)
Rodentia	0.667 (0.640–0.692)	0.742 (0.698–0.789)
Carnivora	0.760 (0.692–0.823)	0.800 (0.721–0.879)
Chiroptera	0.746 (0.687–0.806)	0.817 (0.728–0.905)
Lypothyphla	0.475 (0.401–0.550)	0.587 (0.484–0.691)†
FMR		
Mammalia	0.715 (0.684–0.745)	0.736 (0.675–0.797)
Eutheria	0.755 (0.721–0.789)†	0.766 (0.679–0.853)
Metatheria	0.601 (0.558–0.643)†	0.694 (0.619–0.768)
Rodentia	0.714 (0.599–0.828)	0.766 (0.633–0.899)†

Note: For comparison with slopes of $PGLS_\lambda$ models (λ = ML), see Table 2.

† Equivalent to a $PGLS_\lambda$ model (see Table 2).

body temperature and, as McNab (2006) pointed out, this would erroneously imply that mammals (like ectotherms) have no control over their body temperature. On the other hand, the necessity of controlling for phylogenetic non-independence is well established (Felsenstein 1985, Harvey and Pagel 1991, Martins and Garland 1991, Freckleton et al. 2002). A more robust method for controlling for interspecific differences in body temperature when investigating the allometry of metabolic rates is including body temperature as a predictor in the model. A recent phylogenetically controlled study followed this procedure and showed that body temperature explains only 0.1% additional variance in mammalian BMR (Sieg et al. 2009). Crucially, this study found that, when body temperature is included in the model, the allometric slope of mammalian BMR excludes both 2/3 and 3/4 and varies among lineages, thus reaching very similar conclusions to the ones presented here (Sieg et al. 2009).

Our analysis is independent of biases in size distribution in the data set, since we replicated our tests within orders where size differences are much less pronounced than across all mammals. Furthermore it shows that, among small mammals, true insectivores exhibit lower BMR allometric slope than rodents and bats. This result further speaks against analyses based on binning the data across the whole data set irrespective of phylogeny (as in Savage et al. [2004]). Indeed, we showed that metabolic rates, when tested individually, exhibit a strong phylogenetic signal in mammals and within each lineage. This result is consistent with previous studies that, using the same as well as other methods, found strong phylogenetic signal in metabolic rates, in several physiological traits and in body mass (e.g., Freckleton et al. 2002, Blomberg et al. 2003, Lovegrove 2009). This indicates that part of the variance in metabolic rates is a consequence of shared evolutionary history between extant species.

The strength of the phylogenetic signal of the association of both metabolic rates with body mass, thus of relative metabolic rates, as estimated by the ML λ, was significantly different from both 0 and 1. Indeed, we showed that $PGLS_\lambda$ models provide a better fit to the data than OLS and PIC models, and that assuming an a priori value of $\lambda = 1$ (PIC) or $\lambda = 0$ (OLS) leads to erroneous conclusions. OLS models yielded approximately 30% error rate in the estimate of the slope and PIC had an error rate of approximately 50%. While $PGLS_\lambda$ models show clearly variation in allometric slopes, PIC would erroneously support a 0.75 exponent for almost all clades. Therefore both OLS models (species-level analysis) and methods like PIC are inappropriate statistical tools because they either underestimate (OLS) or overestimate (PIC) the influence of shared ancestry (Freckleton et al. 2002). We suggest that

TABLE 6. Model fit test, comparing $PGLS_\lambda$ models (ML λ) with OLS models ($\lambda = 0$; species-level analysis) and PIC ($\lambda = 1$), for BMR and FMR.

				PGLS vs. OLS			PGLS vs. PIC	
Clade	ML λ	Lh $PGLS_\lambda$	Lh OLS	LR	*P*	Lh PIC	LR	*P*
BMR allometry								
Mammalia	0.85	**370.2**	214.0	312.3	<0.0001	279.0	182.4	<0.0001
Eutheria	0.78	**315.0**	184.3	261.5	<0.0001	234.1	161.8	<0.0001
Metatheria	0.40	**62.3**	**62.0**	0.7	0.409	55.2	14.3	0.0002
Rodentia	0.69	**206.5**	157.2	98.6	<0.0001	160.1	92.7	<0.0001
Carnivora	0.85	**26.3**	20.4	11.8	0.0006	18.4	15.8	<0.0001
Chiroptera	0.23	**43.5**	40.3	6.4	0.0112	25.11	36.7	<0.0001
Lypothyphla	1.00	**28.2**	17.1	22.2	<0.0001	**28.2**	0.0	1.00
FMR allometry								
Mammalia	0.67	**31.6**	16.2	30.7	<0.0001	10.8	41.5	<0.0001
Eutheria	0.41	**15.4**	13.5	3.75	0.053	−1.3	33.4	<0.0001
Metatheria	0.00	**26.6**	**26.6**	0.00	1.00	18.2	16.9	<0.0001
Rodentia	1.00	**11.7**	9.7	4.1	0.042	**11.7**	0.00	1.00

Notes: Competing models are compared with a likelihood ratio test (LR), whose significance is given from a χ^2 distribution with 1 degree of freedom (see *Methods: Phylogenetic signal and estimating allometric exponent*). The best-fitting model has the highest log-likelihood score (Lh). Best models are indicated in boldface type.

previous claims of predominant 3/4 scaling appear to be based on a failure to adequately account for phylogenetic effects.

Importantly we found that the phylogenetic signal of relative metabolic rates was not uniform but varied among lineages. For example, ML λ for relative FMR was high in rodents but equal to 0 in marsupials. There was however no relationship between the allometric slope and ML λ, suggesting that a strong phylogenetic signal does not necessarily lead to a steeper or shallower slope. Intraspecific variation might lead to lower estimates of the phylogenetic signal and a recent method showed that, after accounting for intraspecific variation, estimates of the phylogenetic signal increase (Ives et al. 2007). Plasticity is a source of intraspecific trait variation and metabolic rates are plastic (e.g., Veloso and Bozinovic 1993, Corp et al. 1997, Nespolo et al. 2001, Speakman et al. 2003, Bozinovic et al. 2007, Russell and Chappell 2007). Thus, we suggest that the pattern of variation in the strength of the phylogenetic signal that we have found might indicate that relative metabolic rates are more plastic than absolute metabolic rates, with relative FMR being more plastic than relative BMR, particularly in marsupials.

Suggestions that nonlinear models would better fit the relationship between log-transformed metabolic rates and body mass (e.g., Packard and Birchard 2008) based on species-level tests, are likely to be, at least partially, a consequence of ignoring phylogenetic non-independence between species due to their common evolutionary history. We found little evidence that a polynomial model would better fit the data given that residuals show little curvilinearity and, most importantly, the inclusion of the quadratic term only marginally increased the amount of variance explained. Freckleton (2009) strongly argued against too much faith in small increases in R^2 between models for drawing conclusions on the importance of independent variables. We suggest then that most of deviation from linearity is due to similarity between species due to common ancestry; residuals in fact show significant phylogenetic clustering. Consistent with this explanation, Lovegrove (2000) argued that large residuals of metabolic rates in small and large mammals relative to intermediate-sized mammals are a consequence of ecological factors (e.g., rainfall seasonality and unpredictability affecting resource distribution temporally and spatially) and coevolutionary arms races between predators and prey (for example explaining large BMR residuals of artiodactyls and carnivores).

Overall, our phylogenetically controlled analyses show that the allometric slopes of metabolic rates in mammals are variable and do not consistently support a specific theoretical value, hence extending the proposal of larger-scale taxonomic variability, from unicellular organisms to vertebrates and among metabolic states (Bokma 2004, Glazier 2005, 2008, White et al. 2007*a*). The metabolic theory of ecology (MTE) assumes a predominant 3/4 scaling of metabolic rates (Brown et al. 2004). However, we found that this value was excluded for BMR scaling across all mammals, as well as for one of two infra-classes, and for two of four orders. Similarly, for FMR the 3/4 value was excluded for all mammals, and for one of two infra-classes. We conclude that 3/4 scaling is not predominant in mammals, questioning the empirical basis of the MTE. We also showed that, although the strength of the phylogenetic signal of metabolic rates and body mass is high when tested individually, the strength of the phylogenetic signal of relative metabolic rates is highly variable between clades, perhaps reflecting a greater phenotypic plasticity in some groups. Variability in the strength of the phylogenetic signal among lineages and metabolic rates might lead to erroneous conclusions on the estimate of the allometric exponents when methods that assume a priori a specific value of the phylogenetic signal are used.

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APPENDIX A

References for data in the Supplement (*Ecological Archives* E091-198-A1).

APPENDIX B

Additional tables on the phylogenetic signal of metabolic rates in each lineage (*Ecological Archives* E091-198-A2).

APPENDIX C

Additional figures of the residuals of the metabolic rates on body mass (*Ecological Archives* E091-198-A3).

SUPPLEMENT

Data on basal metabolic rate (BMR) with experimental animal body mass, field metabolic rate (FMR) with wild animal body mass, and sources of the data (*Ecological Archives* E091-198-S1).